

**PUPAL MORPHOLOGY AND THE SUBFAMILY
CLASSIFICATION OF THE NOTODONTIDAE
(LEPIDOPTERA: NOCTUOIDEA)**

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Abstract.—Pupal morphology is surveyed among 46 species of Notodontidae representing all currently-recognized subfamilies, and 24 phylogenetically informative characters are identified. Comparison of a previous notodontid subfamily phylogeny based on larval and adult morphology with one constructed from pupal data shows close concordance. Although it was not possible to identify a synapomorphy for the Notodontidae from pupae, this life stage provides a long list of potential synapomorphies useful at the subfamily level.

The immature stages of Lepidoptera provide crucial character information for studies in taxonomy and phylogeny. Unfortunately, our knowledge of pupal morphology is lagging behind the growing body of data on larvae. This can be attributed, at least in part, to a lack of available material. For example, in the North American Notodontidae, where larvae are known for the majority of species, preserved pupae are relatively uncommon in collections. Among tropical groups, the situation is dismal; in the Neotropical notodontid subfamily Dioprinae, larvae are known for about 4% of the fauna (Miller, 1992), and pupal material is available for less than 2%.

Use of pupal characters has a long history in Lepidoptera systematics. Among the earliest comparative studies are those of Jackson (1890), Poulton (1891), and Chapman (1892, 1893), all of whom stressed the potential taxonomic value of pupae. Early attempts at a phylogeny for the lepidopteran families (Packard, 1895; Chapman, 1896) relied heavily on pupal characters. Hinton's (1946) classification of insect pupae drew attention to the major subdivisions of the Lepidoptera. Pupa figure prominently in modern treatments as well. Minet (1991), in his recent phylogeny for the Ditrysia—by far the largest and most homogeneous part of the order (Nielsen, 1989)—identified several important pupal characters.

The preeminent worker on Lepidoptera pupae was Edna Mosher, whose papers form the basis for study even today. Her research uncovered characters useful in elucidating problematic family interrelationships that were intractable using adult or larval morphology. In addition to providing a general framework for pupal morphology and classification of the Lepidoptera (Mosher, 1916b), her work focused on the families Saturniidae (1914, 1916a) and Sphingidae (1918a). She also published the most comprehensive study available on pupae of the Notodontidae (Mosher, 1918b).

Pupae are taxonomically important in other families of Lepidoptera, an example being the Geometridae (Rindge, 1952; McGuffin, 1987; Bolte, 1990). Nakamura's

(1976) research on pupae of Japanese Lymantriidae treated 33 species in 16 genera. After identifying a set of useful characters, he subdivided the genera and provided a phylogeny. Common (1990), in his recent book on Australian moths, relied extensively on pupae for family-level diagnostic characters, providing pupal illustrations for representatives of all the Australian moth families.

There are distinct differences among lepidopteran groups in the form of the cocoon, in the mode of pupation, and in the method of escape by the adult from the cocoon and pupa (Hinton, 1946; Common, 1975). A well-known example from the Noctuidae is the unusual boat-shaped cocoon found in Sarrothripinae and Nolinae, which provides evidence of relationship between the two subfamilies (Forbes, 1954; Franclemont, 1960; Kitching, 1984).

Differences in cocoon structure and in the mode of pupation can also be found within the Notodontidae (Packard, 1895; Grünberg, 1912). For example, *Cerura* larvae excavate a shallow depression in a twig (usually on the foodplant) and construct an extremely dense cocoon formed from chewed wood particles and salivary secretions (Dyar, 1891; Chapman, 1892). When the adult moth emerges it produces a secretion from the head, possibly containing an enzyme (Kafatos and Williams, 1964), which dissolves the tough cocoon (Chapman, 1892; Hinton, 1946). Dolinskaya (1989) divided notodontids into two groups: those—such as *Cerura*, *Furcula*, *Gluphisia*, and *Clostera*—that pupate on the food plant, and those—such as *Phalera*, *Stauropus*, *Notodonta*, *Pheosia*, and *Spatalia*—that leave the host to pupate in the soil or litter. She further pointed out that in the first group of genera, all except *Clostera* exhibit reduction of the cremaster (see Character 20 below). Although characters relating to cocoon structure and pupation behavior will undoubtedly provide valuable information for future work on notodontid systematics, they were not used here simply because available data are scarce.

This paper is intended to compliment the pioneering works of Packard (1895), Mosher (1916b, 1918b), and Dolinskaya (1989) on notodontid pupae. Those authors demonstrated extensive variation in a variety of characters, and all used pupal traits in their subfamilial and generic diagnoses. However, their findings have not been examined in the context of a world-level classification. In a recent paper (Miller, 1991), I recognized nine subfamilies for the world Notodontidae. My cladistic hypothesis for those is shown in Figure 1. This paper is not a comprehensive treatment of pupae, but it provides an overview with two major aims: to identify potentially useful characters for notodontid phylogeny and classification, and more generally, to stimulate further interest in the morphology of this life stage. In particular, I stress the implications of pupal data for understanding subfamily relationships.

MATERIALS AND METHODS

Morphological terminology (see Fig. 2) follows Mosher (1916b) and Common (1990). Most of the pupae I studied had been preserved in alcohol. Intact pupae were examined in almost all cases, but where these were not available, exuviae were used. Line drawings were made using a camera-lucida attached to a Zeiss SV8 stereomicroscope. Scanning electron micrographs were taken with a Zeiss DSM950 microscope. Specimens for SEM were air-dried, mounted on stubs in silver paste, and then dried again overnight in an oven at 47°C before being coated with gold-palladium.

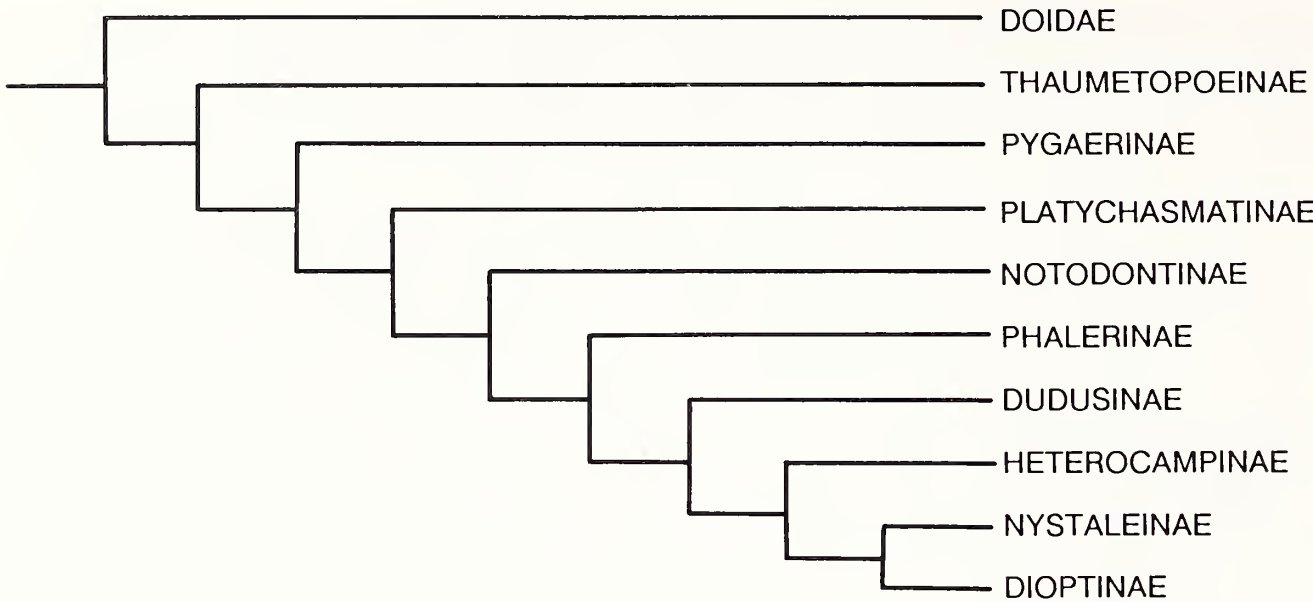


Fig. 1. Cladogram of subfamilies in the Notodontidae based on an analysis of 174 larval and adult characters (from Miller, 1991).

The list of species examined is shown in Table 1. Comprehensive study of outgroup taxa was beyond the scope of this paper. The Doidae—containing two relatively small genera, *Doa* Neumoegen and Dyar and *Leuculodes* Dyar (Franclemont, 1983; Donahue and Brown, 1987)—and Notodontidae are thought to be sister groups (Miller, 1991). I used pupae of *Doa ampla* (Grote) (Fig. 2) for outgroup comparison. The pupa of another doid, *D. dora* Neumoegen and Dyar, was figured by Brown (1990). I have generally relied on Mosher (1916b) in my assessment of pupal morphology among quadrifid Noctuoidea, but needless to say, this is a cursory approach; the group contains tremendous morphological variation, and Mosher’s treatment is relatively brief.

I performed cladistic analyses using pupal characters scored for 16 notodontid species. These 16 taxa were chosen to represent the nine subfamilies recognized in Miller (1991). Twenty-four characters comprising 61 character states (Table 2) were identified. The resulting data matrix (Table 3) was then analyzed using the Hennig86 parsimony program of Farris (1988), with *Doa ampla* as an outgroup. Shortest trees were produced by implicit enumeration. The analysis provides a test of how pupae fit with my previous hypothesis of subfamily relationships based on adult and larval characters (see Fig. 1).

PUPAL MORPHOLOGY

Below is the list of characters for which I found useful variation. My treatment is preliminary; more characters certainly remain to be discovered, and it is impossible to fully assess morphological variation using such a small species sample. However, all the traits I discuss deserve consideration in future taxonomic research on the Notodontidae. Characters with numbers in parentheses were used in the cladistic analyses (see Table 2).

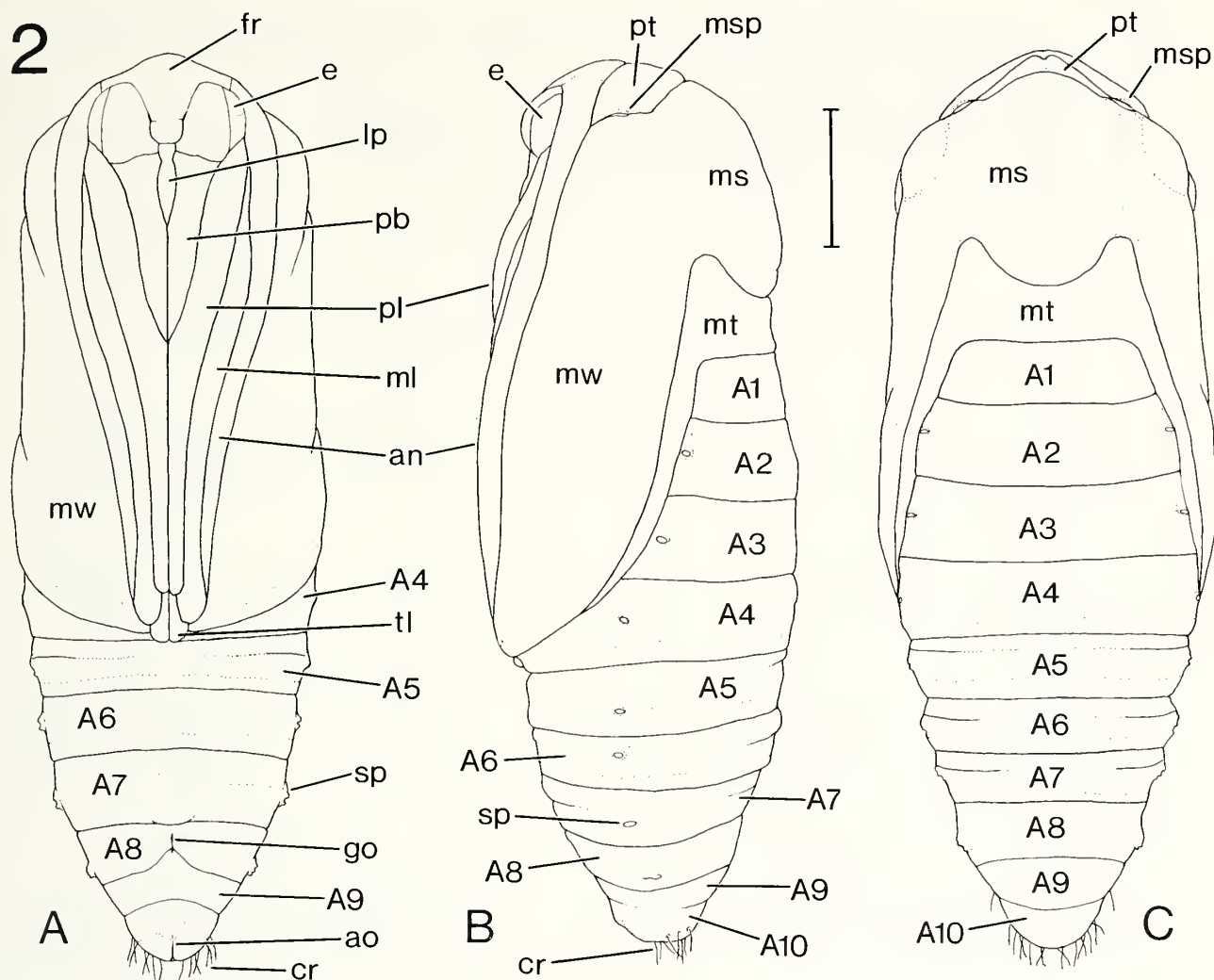


Fig. 2. Pupa of *Doa ampla* (Grote) (Doidae). A. Ventral view. B. Lateral view. C. Dorsal view. A = abdominal segment; an = antenna; ao = anal opening; cr = cremaster; e = eye; fr = front; go = genital opening; lp = labial palpi; ml = mesothoracic leg; ms = mesothorax; msp = mesothoracic spiracle; mt = metathorax; mw = mesothoracic wing; pb = proboscis; pl = prothoracic leg; pt = prothorax; sp = spiracle; tl = metathoracic leg. Scale line = 2 mm.

Head:

Eyes. (1) Mosher (1916b) recognized two parts of the eye in Lepidoptera pupae: one part she termed the “sculptured eye-piece,” and the other the “glazed eye-piece.” I found this division difficult to see, at least in notodontids, and the morphological distinction may be unnecessary for this group.

Mosher (1918b) identified an interesting character in her study of Maine notodontids. She noticed that in *Clostera* species, the proximo-lateral angles of the proboscis do not reach the eye-pieces (Fig. 4A). This is also illustrated by the pupae of *Doa ampla* (Fig. 2A) and *Thaumetopoea pinivora* (Fig. 3A). In most notodontids, the proximo-lateral angles of the proboscis reach the eye-pieces (Figs. 5A, 6A, 8A–12A). In *Cerura* and *Furcula* they do not (Fig. 7A), but in other Notodontinae they do (Fig. 8A). Thus, according to my survey only the Doidae, the Thaumetopoeinae, the Pygaerinae, as well as *Cerura* and *Furcula* of the Notodontinae, exhibit the first

Table 1. List of species for which pupae were examined arranged according to the classification of Miller (1991).

Taxon	Locality	Collection
Doidae		
<i>Doa ampla</i> (Grote)*	Arizona	CUIC
Notodontidae		
Thaumetopoeinae		
<i>Thaumetopoea pinivora</i> (Treitschke)*	Germany	CUIC
Pygaerinae		
<i>Clostera albosigma</i> Fitch*	New York	CUIC, NYSM
<i>C. inclusa</i> Hübner	Illinois	INHS
Platyhasmatinae		
<i>Platyhasma virgo</i> Butler*	Japan	SSC
Notodontinae		
Notodontini		
<i>Notodonta simplaria</i> Graef*	New York	NYSM
<i>Pheosia portlandia</i> Hy. Edwards	Oregon	NYSM
<i>Hyperaeschra georgica</i> Herrich-Schäffer	New York	CUIC
Dicranurini		
<i>Cerura scitisscripta</i> Walker	Florida	AMNH
<i>Furcula occidentalis</i> (Lintner)*	New York	AMNH
<i>F. scolopendrina</i> (Boisduval)	New York	NYSM
<i>F. modesta</i> (Hudson)	New York	NYSM
<i>Gluphisia septentrionis</i> Walker*	New York	AMNH, CUIC
Phalerinae		
<i>Datana robusta</i> Strecker	Texas	CUIC, USNM
<i>D. integerrima</i> Grote and Robinson	New York	CUIC, NYSM
<i>D. ministra</i> (Drury)*	New York	CUIC
<i>D. drexelii</i> Hy. Edwards	New York	CUIC
<i>D. contracta</i> Walker	New York	CUIC
<i>D. angusii</i> Grote and Robinson	New York	CUIC
<i>Phalera</i> sp.**	—	—
<i>Ellida caniplaga</i> Walker	New York	CUIC
<i>Nadata gibbosa</i> Smith	Illinois	INHS, NYSM
Dudusinae		
<i>Crinodes besckei</i> Hübner*	Costa Rica	INHS
<i>Goacampa variabilis</i> Schaus*	Costa Rica	INHS
Heterocampinae		
<i>Heterocampa umbrata</i> Walker	Illinois	INHS
<i>H. bilineata</i> Packard	Illinois	INHS
<i>H. guttivitta</i> Walker*	New York	NYSM
<i>Hyparpax aurora</i> (Smith)	New Jersey	AMNH, USNM
<i>Lochmaeus manteo</i> Doubleday*	New York	NYSM
<i>Misogada unicolor</i> Packard	New York	NYSM

Table 1. Continued.

Taxon	Locality	Collection
<i>Schizura ipomoeae</i> Doubleday	Connecticut	AMNH
<i>S. badia</i> (Packard)	New York	AMNH
<i>S. unicornis</i> (Smith)	New Jersey	AMNH
<i>S. concinna</i> (Smith)	Illinois	INHS
<i>Litodonta hydromeli</i> Harvey	Texas	SJW
<i>Spatalia argentina</i> (Schiffermüller)	Europe	CUIC
Nystaleinae		
<i>Didugua argentilinea</i> Druce*	Texas	USNM
<i>Symmerista albifrons</i> Smith*	Illinois	INHS
<i>S. leucitys</i> Franclemont	New York	NYSM
Dioptinae		
<i>Cyanotricha necyria</i> Felder	Colombia	AMNH
<i>Josia ligula</i> Hübner*	Ecuador	SJW
<i>Phaeochlaena gyon</i> Fabricius	Brazil	BMNH
<i>Phryganidia californica</i> Packard	California	USNM
<i>Zunacetha annulata</i> Guérin*	Panama	AMNH
Incertae Sedis		
<i>Nerice bidentata</i> Walker	New York	NYSM
<i>Lophopteryx cuculla</i> Esper	Germany	CUIC
<i>Drymonia trimacula</i> Esper	Germany	CUIC

*, Species used for the cladistic analyses (see text).
**, Characters for *Phalera* pupae were taken from descriptions and figures in the literature.
Acronyms for collections: AMNH, American Museum of Natural History, New York, NY; BMNH, The Natural History Museum, London, GB; CUIC, Cornell University Insect Collections, Ithaca, NY; INHS, Illinois Natural History Survey, Champaign, IL; NYSM, New York State Museum, Albany, NY; SJW, Susan J. Weller collection, LSU, Baton Rouge, LA; SSC, Shigero Sugi collection, Tokyo, Japan; USNM, United States National Museum, Washington, DC.

character state, while all other taxa show the second. The “primitive” character state in *Cerura*/*Furcula* may not be homologous with others; in both genera, the eye-piece itself is relatively small (see Fig. 7A, B).

Front shape. The front in pupae is defined as the sclerite to which the antennae are attached (Mosher, 1916b). There are various shapes of the front. It is smoothly rounded in most species, whereas it protrudes to varying degrees in others, *Zunacetha annulata* (Dioptinae) (Fig. 12) being an example. The front in *Datana* and *Phalera* species is highly sculpted (Fig. 13; Dolinskaya, 1989).

Some primitive Lepidoptera pupae have a “cocoon-cutter” on the head used to cut through the fabric of the cocoon, but there is no comparable structure in *Ditrysia* (Hinton, 1946). Various notodontids have modifications on the adult head (Miller, 1991) that assist in digging through the substrate upon emergence from the pupa. However, there seems to be no correlation between adult and pupal stages regarding modified heads. For example, notodontids with specializations in adults, such as *Thaumetopoea* and *Goacampa*, show nothing in pupae (Figs. 3, 9). In contrast, the

Table 2. Pupal characters used in a cladistic analysis of sixteen representative notodontid species. Autapomorphic characters were not used, and are omitted from the list.

1. Proximo-lateral angles of the proboscis: not reaching eye-pieces (0); reaching eye-pieces (1).
2. Labial palpus sclerite: present (0); absent (1).
3. Length of proboscis: approximately $\frac{1}{3}$ that of wings, prothoracic legs and mesothoracic legs meeting at midline (0); approximately $\frac{1}{2}$ that of wings, only mesothoracic legs meeting at midline (1); equal to or greater than that of wings, prothoracic and mesothoracic legs not meeting at midline (2).
4. Anterior suture of proboscis: strongly curved, arching forward toward vertex of head (1); not strongly curved and arching forward (0).
5. Antennae: shorter than mesothoracic legs (0); extending beyond mesothoracic legs (1); greatly elongate, extending to A5 (2).
6. Thorax length (ventral view): less than $\frac{2}{3}$ total body length (0); equal to $\frac{2}{3}$ total body length (1).
7. Secondary setae: absent (0); covering thorax and abdomen (1).
8. Dorsum of thorax: smooth or with a small ridge along midline (0); with a distinct crest along midline (1).
9. Sculpturing on caudal margin of mesothorax: not present (0); with a series of shallow depressions separated by raised ridges (1); with a series of small, quadrangular plates separated by deep pits (2).
10. Shape of mesothorax: smoothly rounded dorsally, posterior margin gradual (0); with a dorsal hump, posterior margin projecting at body midline (1).
11. Lateral portions of metathorax: roughly parallel-sided (0); sinuate (1).
12. Thoracic cuticle: smooth or with a few scattered, shallow pits (0); covered with many deep pits (1).
13. Anterior margin of each movable segment (A5–A7): unmodified (0); with a diffuse band of small pits (1); with a single row of lunate pits (2); with a distinct carina (3).
14. Abdominal cuticle: smooth or with fine wrinkles (0); with small pits scattered over the surface (1); covered with large, deep pits (2); covered with large, shallow pits and raised ridges (3).
15. Abdominal spiracles: small (0); large (1).
16. Abdominal spiracle shape: spiracle margins equal in size, spiracle opening laterally (0); anterior spiracular margin more robust and raised, so that spiracle opens posteriorly (1).
17. Segments A8–A10: tapered posteriorly (0); broadly rounded (1).
18. Anterio-dorsal margin of A10: unmodified (0); with a deep furrow (1); sharply elevated, with a lip-shaped edge (2).
19. Dorsum of A10: smooth (0); with a raised, reticulate area anterior to cremaster (1); with numerous, small longitudinal ridges (2).
20. Cremaster: variously shaped (0); bifurcate (1); long and spine-like (2); broad, compressed (3); absent (4).
21. Base of cremaster: smooth (0); fluted (1).
22. Number of cremaster setae: 20 or more (0); between eight and ten (1); setae absent (2); cremaster absent (?).
23. Body: cylindrical (0); dorso-ventrally compressed (1).
24. Body: variously shaped, but roughly elongate (0); wide relative to its length (1).

Table 3. Data matrix of 24 pupal characters (Table 2) for 16 species of Notodontidae (see Table 1) with *Doa ampla* used as an outgroup.

	5	10	15	20	24
<i>Doa</i>	00000	00000	00000	00000	0000
<i>Thaumetopoea</i>	01000	01000	00000	00001	0201
<i>Clostera</i>	00000	01000	10011	00002	0000
<i>Platychasma</i>	10201	00000	10010	00020	0000
<i>Notodonta</i>	11100	00000	10011	01001	0100
<i>Furcula</i>	11000	00000	10011	01004	0?11
<i>Gluphisia</i>	11000	00000	10011	01004	0?11
<i>Datana</i>	11100	01000	10021	00101	0200
<i>Phalera</i>	11100	01000	10021	00101	0200
<i>Goacampa</i>	11210	00110	10331	00000	0100
<i>Crinodes</i>	11210	00110	10311	00201	0100
<i>Heterocampa</i>	11211	00020	10111	00011	0200
<i>Lochmaeus</i>	11211	00020	10111	00011	0200
<i>Symmerista</i>	10211	00000	11211	10001	1100
<i>Didugua</i>	10211	00000	11211	10001	1100
<i>Josia</i>	11212	10001	10010	10003	1100
<i>Zunacetha</i>	10212	10001	10010	10003	1100

head of *Z. annulata* has a tubercle in the pupal stage (Fig. 12) but is unmodified in adults.

Labial palpi. (2) Although the labial palpi can be relatively large in taxa outside the Notodontidae (e.g., *Doa ampla*, Fig. 2A), they are either highly reduced or absent among notodontids (Mosher, 1916b, 1918b; Common, 1990; Minet, 1991). Most commonly they are absent, but a small, triangular labial palpus sclerite occurs among various notodontid subfamilies (Dolinskaya, 1989) including the Platychasmatinae (Fig. 5A), Nystaleinae (Fig. 11A), and Dioptinae (Fig. 12A).

It is interesting that, contrary to modern ideas, Mosher’s concept of the Noctuoidea excluded the Notodontidae. She placed notodontids in a separate superfamily, the Notodontoidea, along with the Geometridae. Unfortunately, there is still no pupal character known, comparable to the metathoracic tympanum in adults, that can be used to define the Noctuoidea (as the term is currently applied). Mosher (1916b, 1918b) grouped the Notodontidae and Geometridae together because in both the pupae lack labial palpi, but instead have only “a very small triangular or polygonal area” (1916b:125) remaining. Adult and larval data certainly do not support Mosher’s phylogenetic hypothesis (see Miller, 1991; Minet, 1991).

Length of proboscis. (3) Mosher (1916b) used the term maxillae for the proboscis of Common (1990); I follow the latter. Both authors noted that, although highly variable in length, the proboscis is always visible in Lepidoptera. In notodontids, extremes range from the thaumetopoeines, where the proboscis is less than 1/3 the length of the mesothoracic wings (Fig. 3A), to the Dioptinae, where it can extend beyond the caudal margin of the wings, actually touching A5 (Fig. 12A). I divided the character into three states (Table 2). In species with an extremely short proboscis,

the prothoracic and mesothoracic legs meet at the ventral midline (Figs. 3A, 4A, 7A, 8A). In taxa such as *Datana* and *Notodonta*, with a tongue only slightly shorter than the thorax, the mesothoracic legs meet at the midline but the prothoracic ones do not (Fig. 6A; Mosher, 1918b). Finally, in long-tongued species (Figs. 5A, 9A–12A) neither pairs of legs meet along the midline (Mosher, 1918b; Dolinskaya, 1989).

This character has been noted by all authors since Packard (1895). However, proboscis length in pupae can vary greatly even within notodontid subfamilies. For example, there are heterocampine species in which the tongue is as long as the wings (Fig. 10A), and species where the proboscis is much shorter than the wings. Similar variation occurs in the Nystaleinae. It is not surprising that tongue length in pupae is correlated with that in adults (Poulton, 1891).

Anterior sutures of proboscis. (4) I here define the “anterior sutures” of the proboscis as the sutures where the base of the proboscis and the head join (see Figs. 10, 11). In most species, these either arch slightly forward at their midpoint (Fig. 3A), or are straight with an orientation essentially perpendicular to the body midline (Fig. 8A). Four subfamilies of the Notodontidae—the Dudusinae, Heterocampinae, Nystaleinae, and Dioprinae—exhibit a different configuration. In these, the anterior sutures of the proboscis are strongly curved, bending toward the vertex of the head, with the proximo-medial angles of the proboscis being narrow (Figs. 9A–12A).

Length of antennae. (5) Like the proboscis, the antennae of pupae vary in length. In addition, the antennae can either be shorter than the mesothoracic legs or they can extend beyond the mesothoracic legs. The former is typical of most notodontids (e.g., Fig. 9A) as well as their sister group, *Doa* (Fig. 2A), while the latter appears to be restricted to the Platychasmatinae (Fig. 5A), Heterocampinae (Fig. 10A), Nystaleinae (Fig. 11A) and Dioprinae (Fig. 12A). Mosher (1916b), based on study of *Phryganidia californica*, listed long antennae, touching A5, as a diagnostic trait for the Dioprinae. This character state occurs in all the dioprines I examined.

Thorax:

Thorax length. (6) Dioprinae are unusual in that the thorax is elongate. In the species I studied, the thorax is $\frac{2}{3}$ the total body length (Fig. 12), whereas in other notodontids the thorax is less than $\frac{2}{3}$ the body length (e.g., Figs. 3, 5, 10).

Secondary setae. (7) There are primary setae on the body in pupae analogous to the primary setae in larvae (Common, 1990). Those of pupae are small and difficult to locate (Mosher, 1916b). The primary setae of *Zunacetha annulata* (Fig. 12) are large compared to the other species I examined; usually they are microscopic. I did

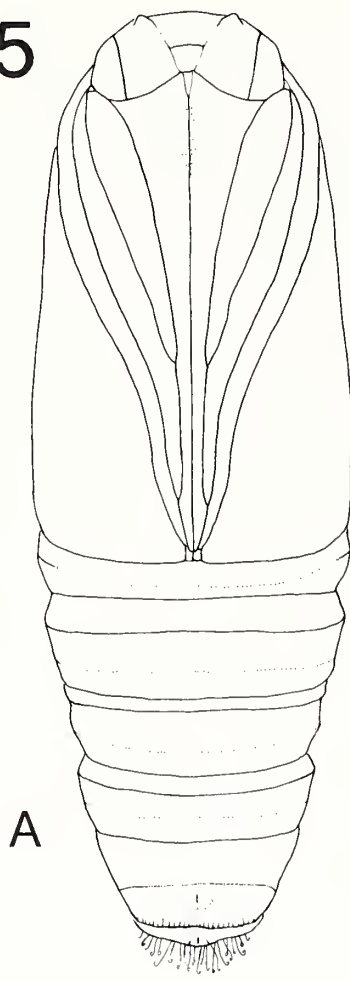
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Figs. 3, 4. Pupae of Notodontidae. 3. *Thaumetopoea pinivora* (Treitschke). 4. *Clostera albosigma* Fitch. A. Ventral view. B. Lateral view. C. Dorsal view. Scale lines = 3 mm.

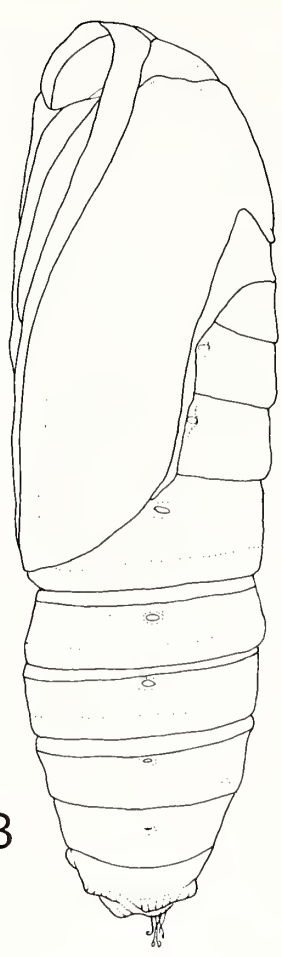
Figs. 5, 6. Pupae of Notodontidae. 5. *Platychasma virgo* Butler. 6. *Datana robusta* Strecker. A. Ventral view. B. Lateral view. C. Dorsal view. Scale lines = 3 mm.

Figs. 7, 8. Pupae of Notodontidae. 7. *Furcula scolopendrina* (Boisduval). Scale line = 3 mm. 8. *Gluphisia septentrionis* Walker. Scale line = 2 mm. A. Ventral view. B. Lateral view. C. Dorsal view.

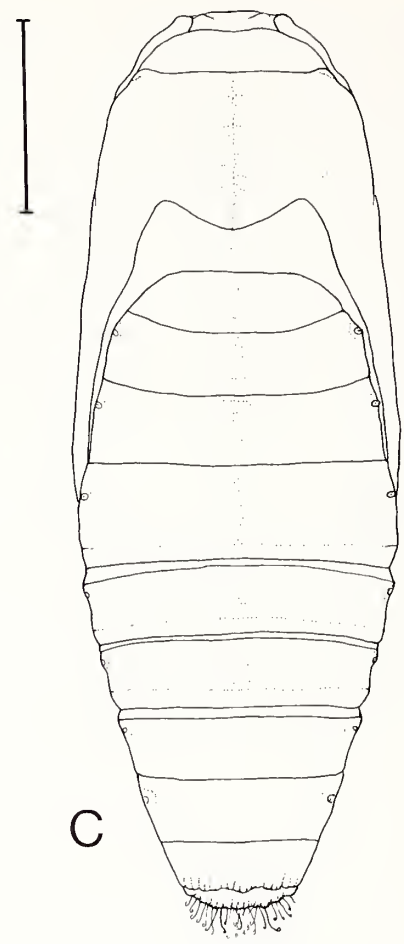
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A

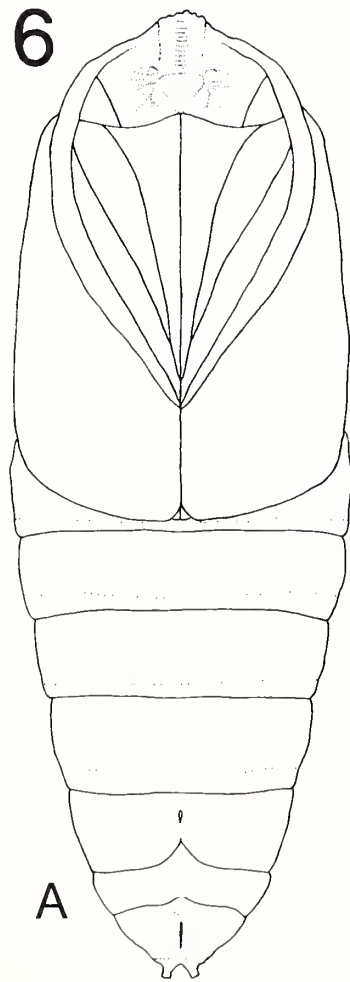


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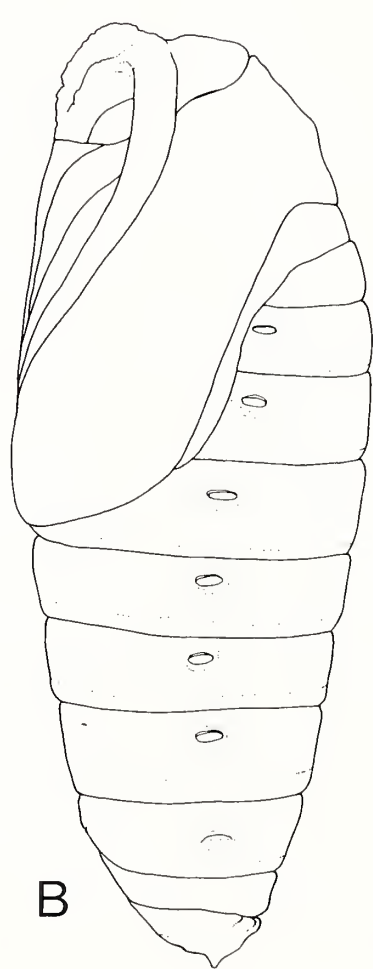


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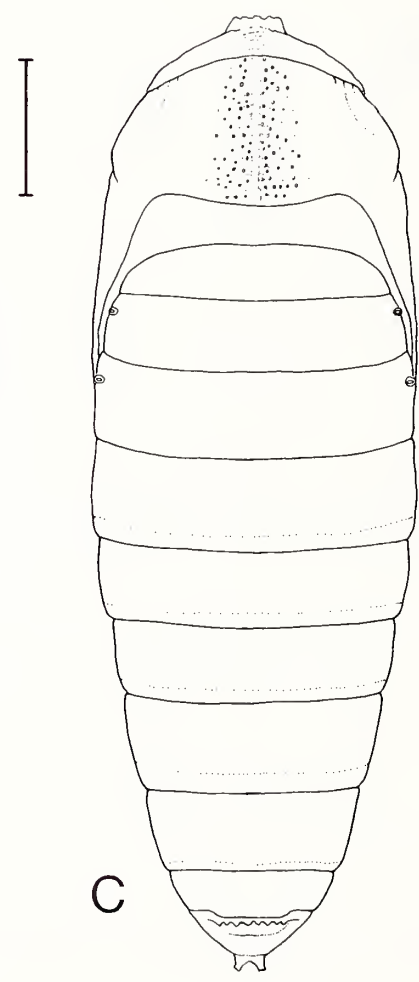
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A

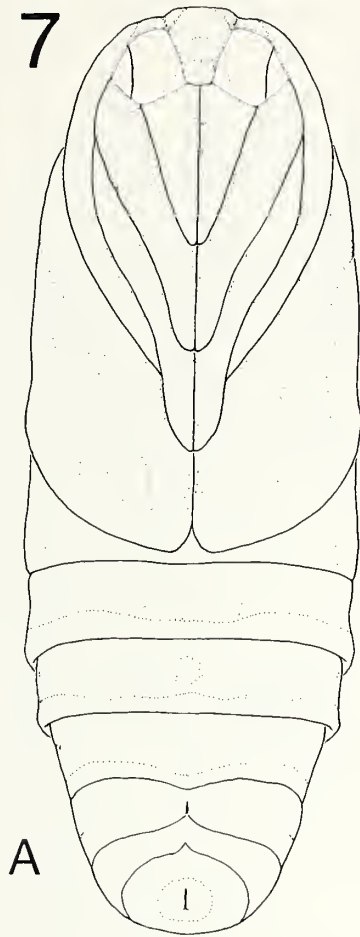


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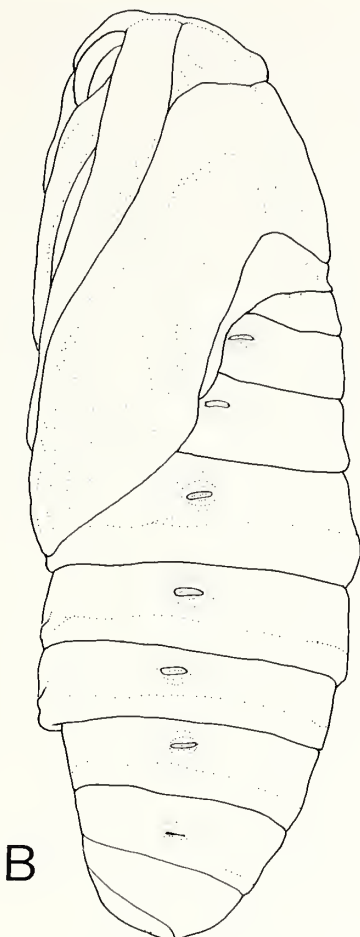


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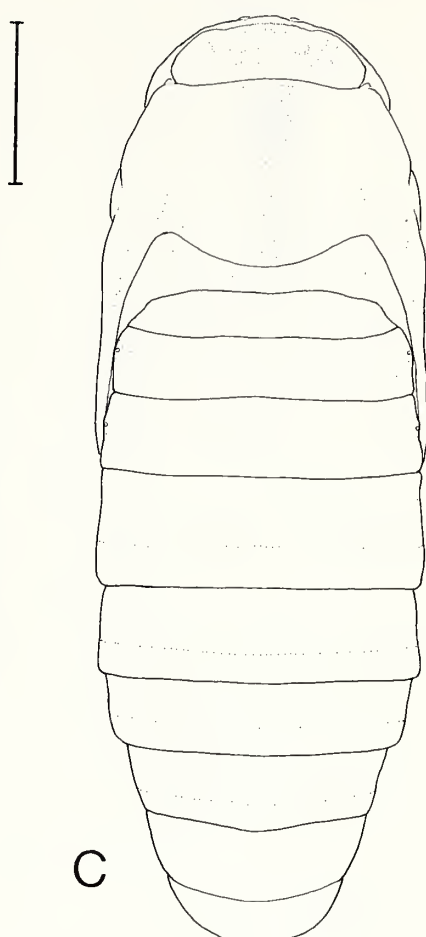
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A

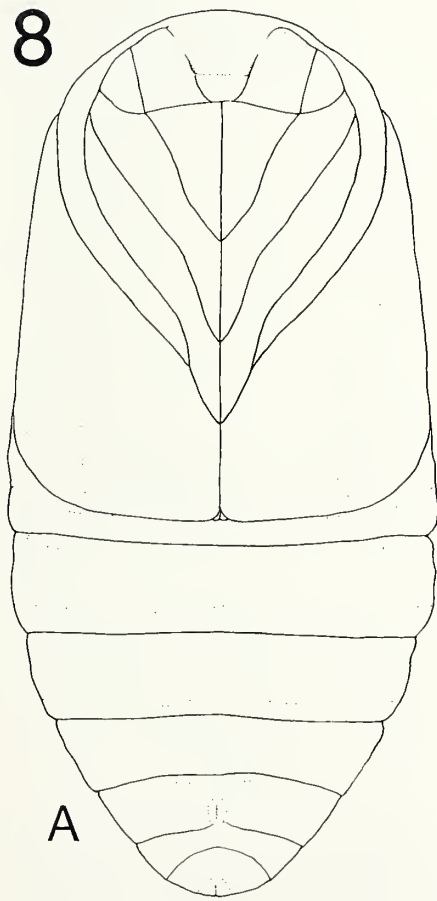


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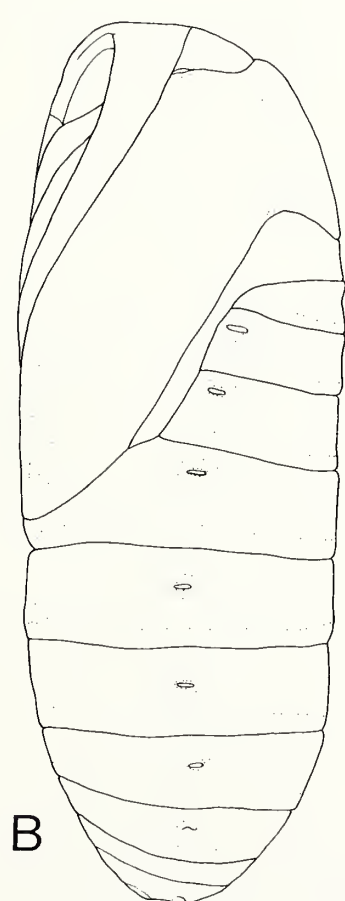


C

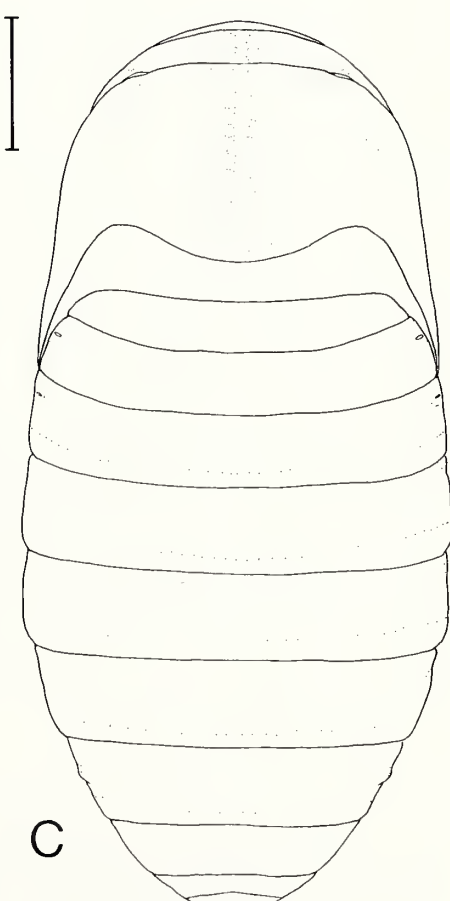
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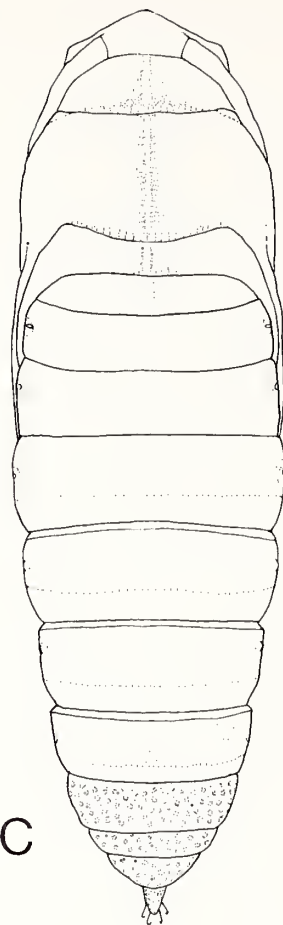
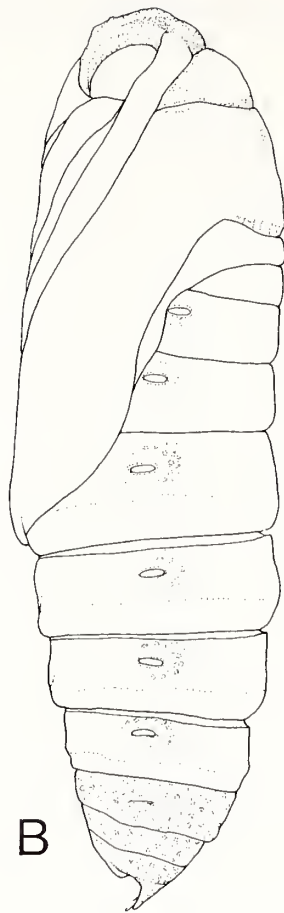
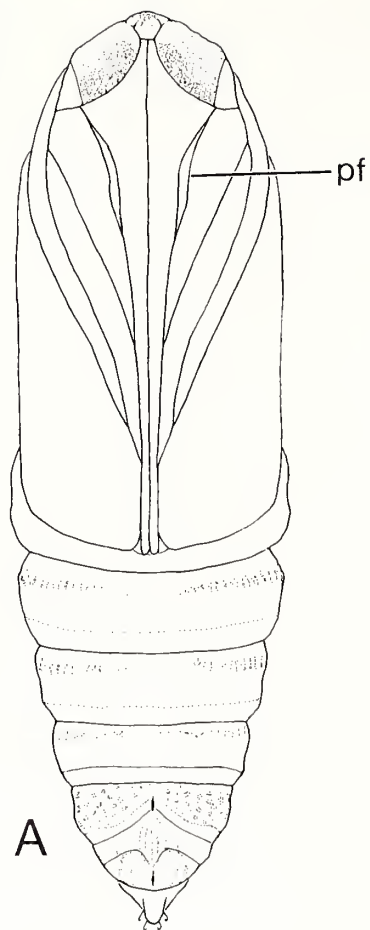


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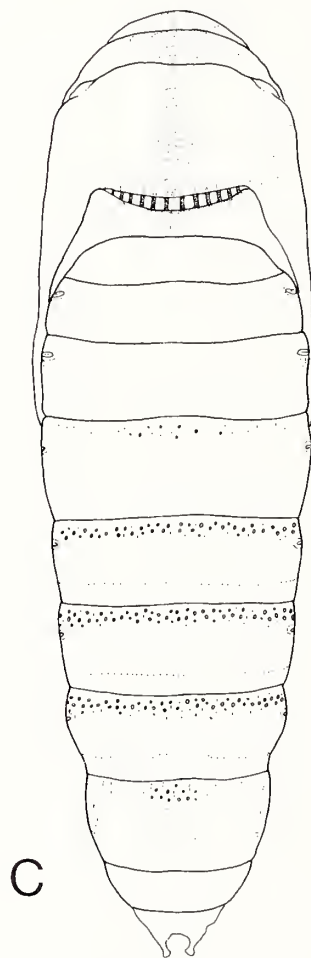
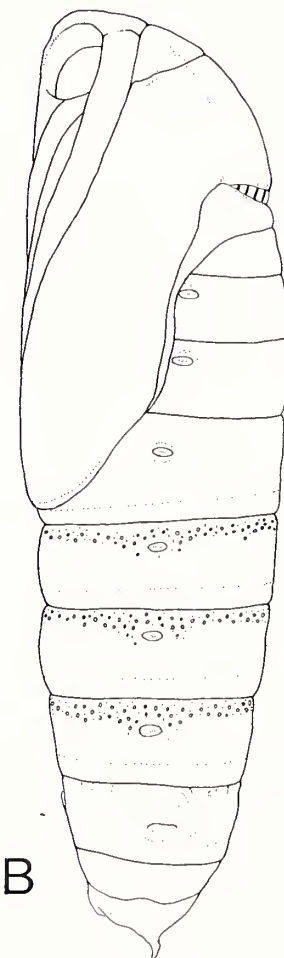
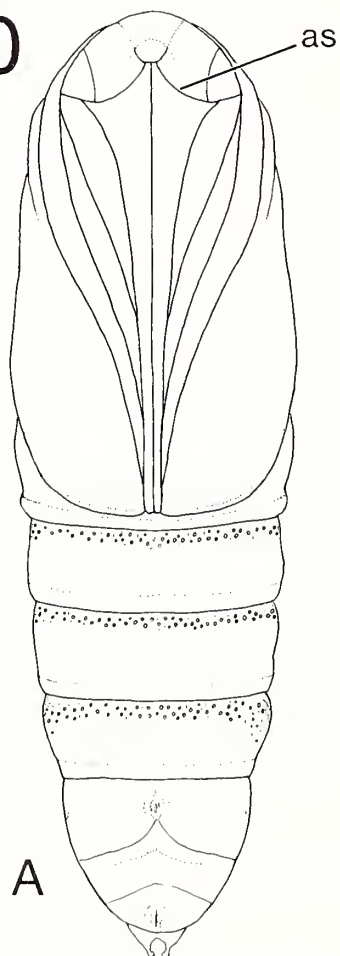


C

9



10



Figs. 9, 10. Pupae of Notodontidae. 9. *Goacampa variabilis* Schaus. 10. *Lochmaeus manteo* Doubleday. A. Ventral view. B. Lateral view. C. Dorsal view. as = anterior suture; pf = femur of prothoracic leg. Scale lines = 3 mm.

not examine primary setal patterns in pupae, but such research might be valuable. They have rarely been used for taxonomic purposes.

Secondary setae can also occur. For example, larvae and pupae of Lymantriidae are covered with long secondary setae (Poulton, 1891; Nakamura, 1976). The relationship between presence or absence of secondary setae in the larval and pupal stages of Notodontidae is interesting. This character shows a high level of homoplasy in larvae; secondary setae occur in caterpillars of the Thaumetopoeinae, Pygaerinae, Phalerinae, Nystaleinae, Dioprinae, and Dudusinae, and each of these cases is thought to have evolved separately (Miller, 1991). Presence of secondary setae in the pupal stage appears to exhibit a more restricted taxonomic distribution. Genera such as *Cyanotricha* (Dioprinae) and *Dasylophia* (Nystaleinae) have secondary setae in larvae but not in pupae. Based on the notodontid pupae I examined, secondary setae occur only in the subfamilies Thaumetopoeinae, Pygaerinae, and Phalerinae. Undoubtedly, examples in other subfamilies will eventually be found. Secondary setae in notodontid pupae are extremely short, almost microscopic (Mosher, 1918b).

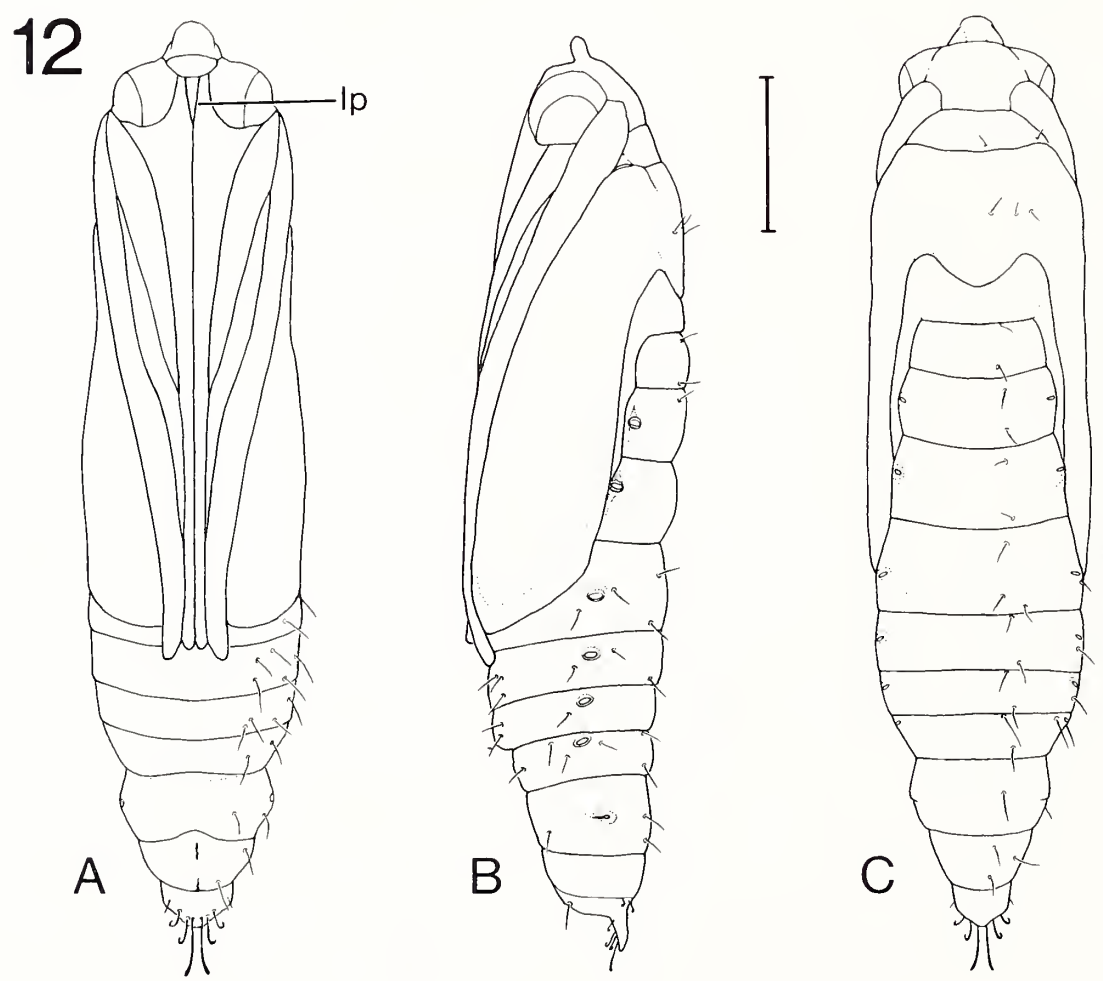
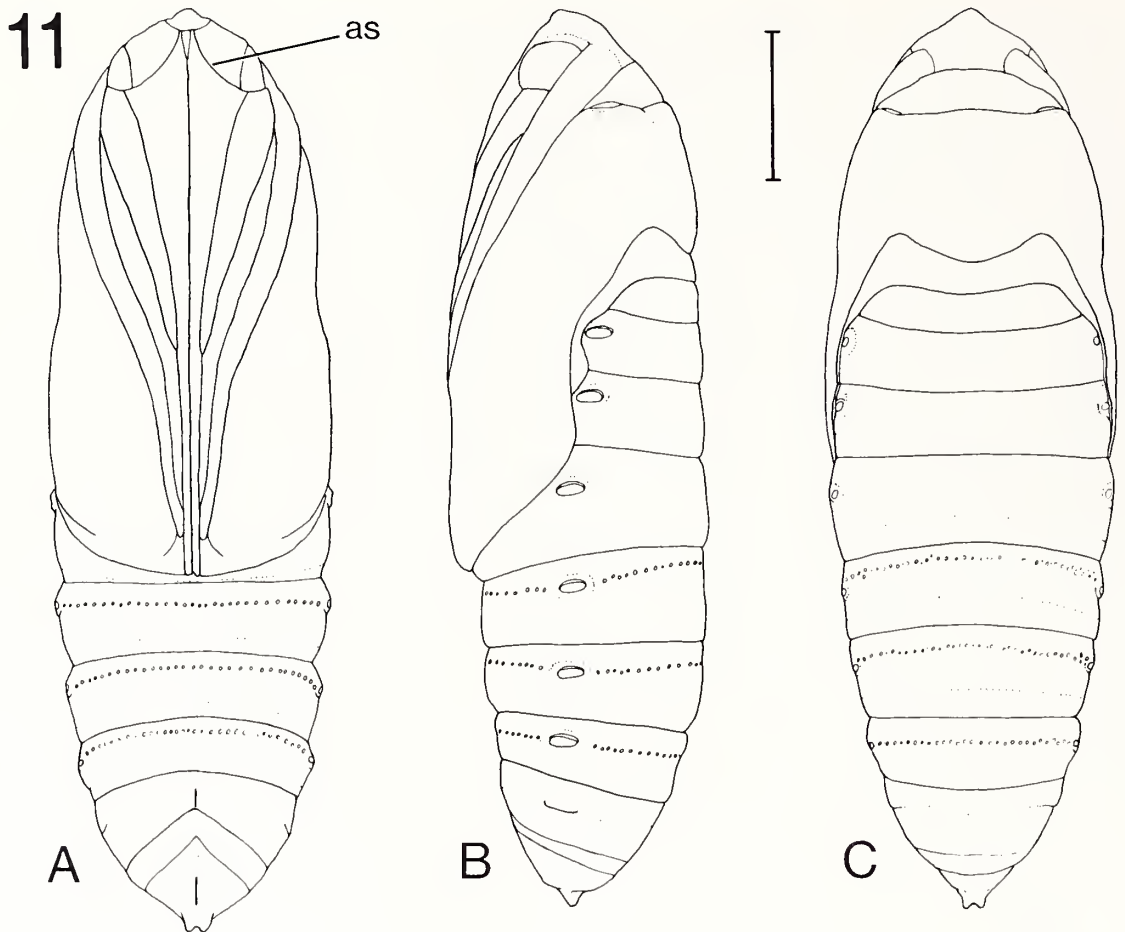
Femur of prothoracic legs. Both Common (1990) and Mosher (1918b), in their diagnoses for the family, stated that the femur of the prothoracic leg is never visible in pupae of Notodontidae. The structure is frequently visible in various other families. I found that the profemur can be seen in at least one notodontid species, *Goacampa variabilis* (Dudusinae) (Fig. 9A). This is obviously a derived character state for the Notodontidae, but without examining additional species its usefulness for phylogeny is unknown.

Prothoracic crest. (8) In the two dudusines I studied, *Crinodes besckei* and *Goacampa variabilis*, there is a distinct crest along the midline on the dorsum of the mesothorax (Fig. 14). It is present, but less obvious, on the prothorax as well. Although a few other taxa show a slightly raised area along the midline (e.g., Figs. 3C, 10C), it is not pronounced.

Mesothoracic spiracle. The shape of the mesothoracic spiracle varies among species (Mosher, 1916b), with sculpturing around the spiracle showing the most significant differences. Unfortunately, thorough study would require SEM for all taxa, something beyond the scope of this paper.

Pits on mesothoracic caudal margin. (9) On the dorsum of the pupa some taxa exhibit modifications of the mesothoracic caudal margin. The most remarkable of these occurs in the Heterocampinae (Fig. 10C). Here, there is a row of from six to twelve small, quadrangular plates separated by deep pits (Figs. 15–17). The plates are slightly convex (Fig. 16) and their surfaces are rugose under high magnification (Fig. 18). This apomorphy, first mentioned by Dyar (1889) and described by Packard (1895) in species of North American Heterocampinae, has been noted by most subsequent authors. Based on my study and on reports in the literature, the trait is restricted to Heterocampinae but is quite widespread within the subfamily, occurring in at least nine genera (Dyar, 1889; Packard, 1895; Mosher, 1916b, 1918b; Weller, 1987; Dolinskaya, 1989). Its function is unknown.

A similar, but less spectacular, modification can be found in *Goacampa variabilis* and *Crinodes besckei* (both Dudusinae). In these species, the caudal margin of the mesothorax bears a row of shallow depressions separated by raised longitudinal ridges (Figs. 9C, 14). Although the character in Heterocampinae and Dudusinae may be homologous, the character states in the two groups are clearly separable.





Figs. 13, 14. Scanning electron micrographs of notodontid pupae. 13. Front of *Datana ministra* (Drury), ventral view (500 μ m). 14. Meso- and metathorax of *Goacampa variabilis* Schaus, dorsal view with anterior at top (500 μ m). Scale lengths in parentheses.

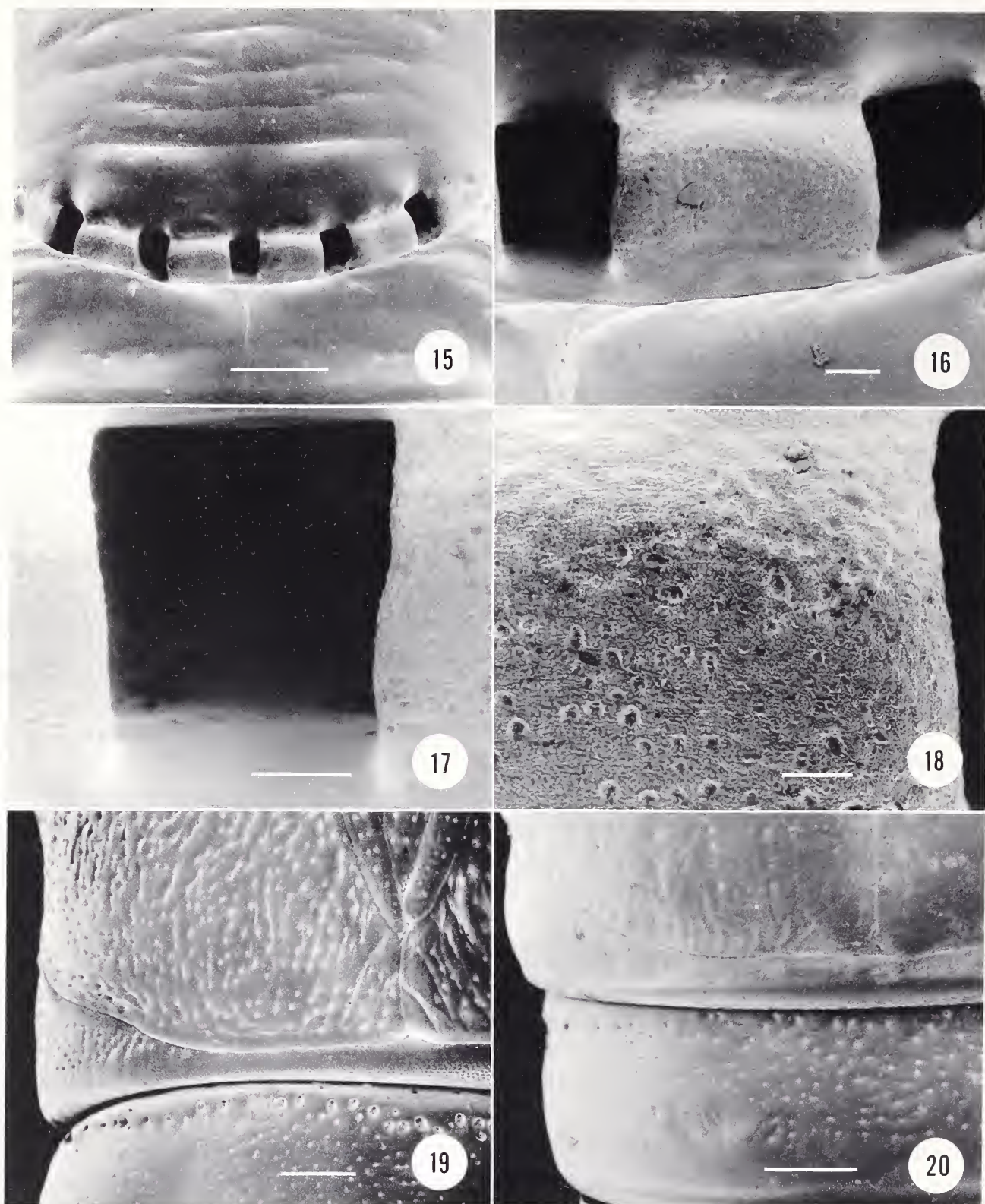
Shape of mesothoracic caudal margin. (10) A modification of the mesothoracic caudal margin, not related to sculpturing, occurs in pupae of Dioptinae. Here, the mesothorax is humped posteriorly and its caudal margin projects sharply posteriad at the body midline (Fig. 12C; Mosher, 1916b). In other notodontids, the caudal margin of the mesothorax forms a shallow curve posteriorly (e.g., Fig. 11C). The derived state seems to provide yet another synapomorphy for the Dioptinae.

Lateral extensions of metathorax sinuate. (11) In all pupae I studied except *Doa ampla* and *Thaumetopoea pinivora*, the lateral extensions of the metathorax have a constriction opposite the A2 spiracle and an expanded distal portion (e.g., Figs. 9B, 11B). This configuration is more marked in some taxa than in others, but it seems to define a monophyletic group that includes all notodontid subfamilies except the Thaumetopoeinae.

The length of the lateral portions of the metathorax also varies among Notodontidae. In some species they extend as far posteriad as A4, either touching the anterior margin of that segment (e.g., *Thaumetopoea pinivora*, Fig. 3B) or extending beyond it (e.g., *Platychasma virgo*, Fig. 5B). In other taxa, they extend only as far as the middle of A3 (e.g., *Goacampa variabilis*, Fig. 9B). However, this character shows so much homoplasy that its value is questionable.

Forewing venation. In most Ditrysia, the only wings visible in the pupa are the forewings (Mosher, 1916b). The trifold Noctuoidea, to which the Doidae and Notodontidae belong (Miller, 1991), have the forewing cubital vein three-branched (comprising veins CuA₁, CuA₂, and M₃), a plesiomorphic trait. The derived state is the quadrifid condition, where M₂ branches from the cubital as well. These veins are usually difficult to see in pupae, except during later development when the pharate

Figs. 11, 12. Pupae of Notodontidae. 11. *Didugua argentilinea* Druce. Scale line = 3 mm. 12. *Zunacetha annulata* Guérin. Scale line = 2 mm. as = anterior suture; lp = labial palpi. A. Ventral view. B. Lateral view. C. Dorsal view.



Figs. 15–20. Scanning electron micrographs of notodontid pupae. 15. Posterior margin of mesothorax in *Heterocampa guttivitta* Walker, dorsal view (400 μm). 16. A single plate from the structure in Figure 15 (50 μm). 17. A pit between plates (40 μm). 18. Surface structure of a single plate (20 μm). 19. *Symmerista leucitys* Franclemont ventral view, showing bottom of wing and segments A4–A5 on right side; tips of antennae in upper right (500 μm). 20. Similar view of *Ellida caniplaga* (500 μm). Scale lengths in parentheses.

adult can be seen through the pupal cuticle. Nevertheless, the trifid condition can be used to separate pupae of the Doidae and Notodontidae from other Noctuoidea. There is one exception; the subfamily Platychasmatinae, containing the monobasic genus *Platychasma*, is the only notodontid group in which the forewing is quadrifid (Nakamura, 1956; Miller, 1991).

Cuticle surface structure. (12) Thoracic surface structure seems to vary independently of that on the abdomen. The nystaleine pupae I examined are characterized by numerous, deep pits covering the thorax (Fig. 19). The thorax of other notodontids either has a few shallow pits scattered over its surface (e.g., *Ellida caniplaga*; Fig. 20), or is smooth.

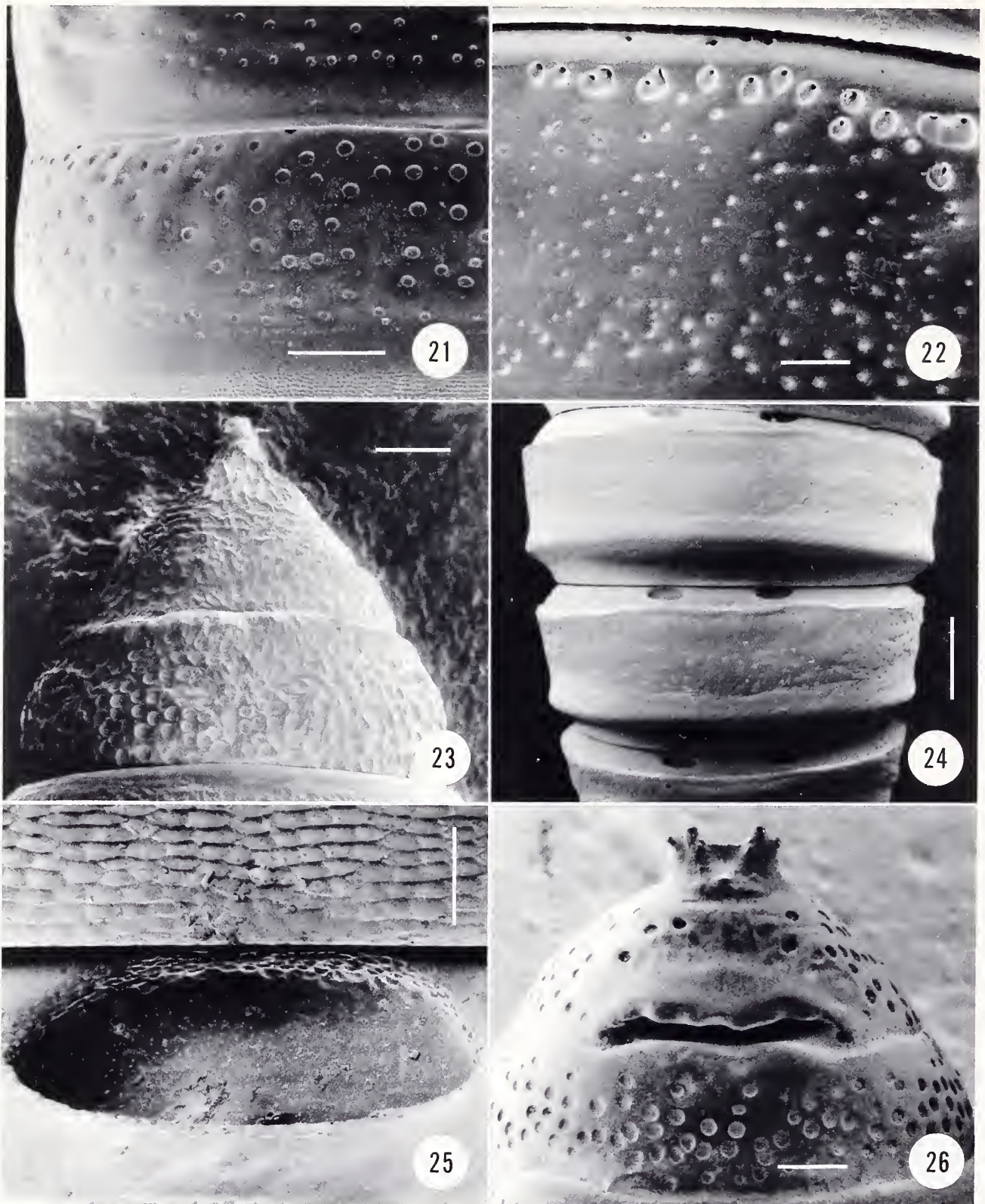
Appendages standing out in relief. In most notodontid pupae the appendages are fused together to form a relatively flat surface. In *Cerura* and *Furcula*, the proboscis, legs, and antennae stand out in relief from the body surface (Mosher, 1916b), a character state also noted by Dolinskaya (1989) for the Palearctic genera *Harpyia* and *Ptilophora*. I placed *Ptilophora* in the subfamily Notodontinae along with *Cerura* and *Furcula*, but I put *Harpyia* in the Heterocampinae (Miller, 1991). The derived state is not found in other Notodontinae, such as *Gluphisia* and *Notodonta* (Dolinskaya, 1989). This trait needs further study.

Abdomen:

The movable segments (A5–A7). (13) In primitive Lepidoptera, abdominal segments A1–A7 are movable, while A8–A10 are always fused (Mosher, 1916b). In more advanced families, such as the Notodontidae, the only movable segments of the abdomen are A5–A7 (Mosher, 1918b). Segments A1–A4 show little morphological variation among notodontid species. The movable segments, on the other hand, often exhibit unique structural modifications not found on other abdominal segments. Segments A9 and A10, bearing the cremaster, show extreme variability (see Character 20).

Various types of specializations can be found along the anterior margin of the movable segments in Notodontidae. The traits appear to provide valuable phylogenetic information, especially useful at the subfamily level. Among more primitive notodontid subfamilies, the movable segments are not modified (e.g., Figs. 3, 7, 8). In advanced groups, however, at least four discrete character states occur: Heterocampine pupae have a diffuse band of small pits ringing the anterior margin of each movable segment (Figs. 10, 21). Nystaleine pupae have a single row of lunate pits (Figs. 11, 22). Mosher (1918b) first described this trait for *Symmerista*, but it occurs in other Nystaleinae as well. Finally, in Dudusinae there is a sharp carina near the anterior margin of each movable segment (Fig. 9). A similar carina can be found in *Hyperaeschra georgica* (Fig. 24). This species has long been placed in the subfamily Notodontinae (Packard, 1895). If that placement is correct, the carina has evolved there independently.

Cuticle structure. (14) Various authors have characterized the abdomen in Notodontidae as being punctate (Mosher, 1918b; Marumo, 1920; Common, 1990). I did not survey abdominal surface structure in detail, but there is considerable variation among species. The cuticle surface of *Doa ampla* and *Thaumetopoea pinivora* is smooth or somewhat wrinkled, without punctations. In other groups, small punctations are the general rule (Figs. 19–22), but in *Datana* and *Phalera* (both Phalerinae),



Figs. 21-26. Scanning electron micrographs of notodontid pupae. 21. Segment A4 of *Heterocampa guttivitta* Walker, dorsal view with anterior at top (500 μ m). 22. Segment A5 of *Symmerista leucitys* Franclemont, ventral view with anterior at top (200 μ m). 23. Terminal segments of *Goacampa variabilis* Schaus, dorsal view with posterior at top (500 μ m). 24. Segments A4-A7 of *Hyperaeschra georgica* Herrich-Schäffer, dorsal view with anterior at top, showing paired pits (1 mm). 25. A single pit on A6 of *H. georgica* (100 μ m). 26. Segments A8-A10 of *Datana ministra* (Drury), dorsal view with posterior at top, showing furrow on A10 (500 μ m). Scale lengths in parentheses.

the abdomen is covered with large pits (Fig. 26; Dyar, 1891; Dolinskaya, 1989). The abdomen of *Goacampa variabilis* exhibits complex surface sculpturing, with shallow pits and furrows (Fig. 23). This character shows variation analogous to that on the surface of the larval head (see Miller, 1991). Like that character, SEM study across a wide variety of species would be valuable.

Paired pits on A5–A7. In *Hyperaeschra georgica*, there is a pair of large dorsal pits on the anterior margin of A5–A7 (Figs. 24, 25). The character is distinctive, but I observed it only in this species. I have not seen reference to these structures in the literature, and their function is unknown.

Spiracle size. (15) The abdominal spiracles are found laterally on segments A2–A8 (Fig. 2B). The one on A8 is always smaller than others, and according to Mosher (1916b) it is not functional. The abdominal spiracles show size variation across taxa. I simply scored them as being either large or small; a more detailed analysis is needed. Small spiracles occur in Doidae, Thaumetopoeinae, Platychasmatinae, and Dioptinae (Figs. 2B, 3B, 5B, 12B).

Spiracle shape. (16) I used one character involving spiracle shape. In Dioptinae and Nystaleinae, the anterior margin of each abdominal spiracle is more robust and heavily sclerotized. Furthermore, this margin is raised so that the spiracular opening faces somewhat posteriorly rather than laterally, the typical orientation.

There are also differences in the sculpturing around the spiracle (Mosher, 1918b). For example, some species have the entire spiracle raised from the body surface (Fig. 2A). This is yet another character that would benefit from comprehensive SEM study.

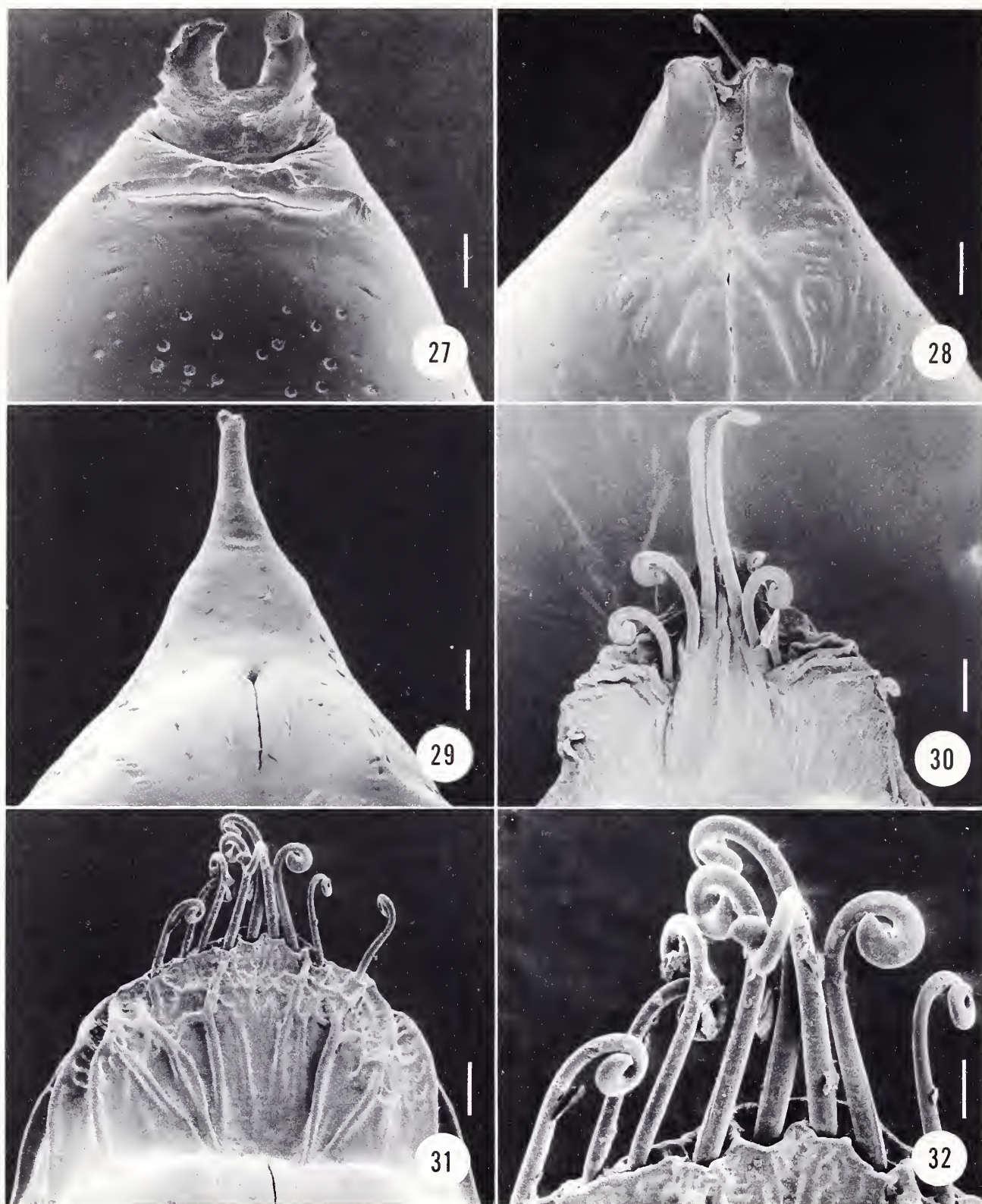
Shape of segments A8–A10. (17) Pupae in the subfamily Notodontinae show a great deal of morphological variation. One potential synapomorphy involves the shape of the terminal abdominal segments (A8–A10), which are broadly rounded (Figs. 7, 8) rather than being tapered as in other Notodontidae. Many notodontines have lost the cremaster, and these exhibit the rounded abdomen. However, the trait also occurs in taxa, such as *Notodonta*, where the cremaster is present (Ferguson, 1963).

Male and female pupae exhibit different external morphologies on the venter of the terminal segments, allowing one to distinguish the sexes (Jackson, 1890; Poulton, 1891; Mosher, 1918b). However, I did not examine this character complex from a taxonomic standpoint because often, specimens of only a single sex were available for study.

Anterior margin of A10. (18) In *Datana* and *Phalera* pupae, the anterior margin of A10 on the dorsal side bears a deep furrow (Poulton, 1891; Nagano, 1916; Mosher, 1918b; Dolinskaya, 1989). The posterior edge of this furrow is often sculpted (Fig. 26). Judging from the species I examined and figures in the literature, there is inter-specific variation in shape. *Datana* species are extremely difficult to separate based on adult characters, so it would be interesting to see whether differences in furrow shape provide valuable species-specific characters.

There is an analogous modification in pupae of *Crinodes besckei*, where instead of a deep furrow, the anterior margin of A10 is sharply elevated and lip-shaped. This character does not occur in the other dudusine I examined, *Goacampa variabilis* (Figs. 9C, 23).

Reticulate area on A10. (19) Some pupae have a sharply raised, reticulate area on the dorsal surface of segment A10 just anterior to the cremaster. This structure was



Figs. 27–32. Scanning electron micrographs of notodontid pupae. 27. Cremaster and A10 of *Heterocampa guttivitta* Walker, dorsal view (200 μ m). 28. Cremaster and A10 of *Symmerista leucitys* Franclemont, ventral view (200 μ m). 29. Cremaster and A10 of *Ellida caniplaga* Walker, ventral view (200 μ m). 30. Cremaster of *Zunacetha annulata* Guérin, ventral view (100 μ m). 31. Cremaster of *Josia ligula* Hübner, ventral view (100 μ m). 32. Cremaster setae of *J. ligula*, ventral view (50 μ m). Scale lengths in parentheses.

discussed for two Palearctic species, *Fentonia ocypete* Bremer and *Spatalia argentina*, by Dolinskaya (1989). It also occurs in *Hyparpax perophoroides* (Strecker) (Ferguson, 1963) and *Misogada unicolor*. All these taxa belong in the subfamily Heterocampinae (Forbes, 1948; Miller, 1991). In *Heterocampa guttivitta*, this reticulate area consists of a few laterally oriented ridges (Fig. 27). In some heterocampines it is absent altogether. *Platychasma* has numerous, small longitudinal ridges on segments 9 and 10 (Fig. 5C), but these are probably not homologous with the structure in Heterocampinae.

Cremaster shape. (20) There is almost endless variation in cremaster morphology among Notodontidae; my study does not begin to tap the structure's taxonomic potential. Proper treatment of this character complex would require a monograph in itself. My goal here is to describe some of the variation, and to begin outlining ways in which the various character states might be useful for phylogenetic purposes.

In species belonging to at least six subfamilies—the Thaumetopoeinae, Notodontinae, Phalerinae, Dudusinae, Heterocampinae, and Nystaleinae—the cremaster is bifurcate (e.g., Figs. 3, 27, 28). There may be examples in other subfamilies as well. I apply a broad definition to this term, scoring any cremaster as bifurcate whose parts are divergent. A bifurcate cremaster may be the ground-plan state for the entire Notodontidae. The distinctive fork-shaped cremaster of Heterocampine (Figs. 10, 27) has been noted by various authors (Packard, 1895; Mosher, 1918b; Marumo, 1920; Ferguson, 1963), and it seems to be a definitive subfamily trait, at least for Holarctic species. A bifid cremaster with spiny projections (Fig. 26) is characteristic of *Datana* and *Phalera* (Dyar, 1891; Poulton, 1891; Mosher, 1918b).

Other cremaster types include the long, spine-like cremaster of *Clostera* (Packard, 1895; Nagano, 1916; Mosher, 1918b) and *Ellida* (Fig. 29), and the broad, compressed cremaster of Dioprinae (Figs. 30, 31).

Finally, there are notodontid pupae where the cremaster is entirely absent. This was described over a hundred years ago by Poulton (1891) and Dyar (1891) for species of *Cerura* and *Furcula* (Notodontinae), and has subsequently been discussed by other workers (e.g., Packard, 1895; Dolinskaya, 1989). In these species, the ninth and tenth abdominal segments are broadly rounded and the abdomen is completely smooth posteriorly (Fig. 7). An almost identical condition occurs in the genus *Gluphisia* (Packard, 1895; Ferguson, 1963; Dolinskaya, 1989; Fig. 8). I previously made the suggestion (based on larvae and adults) that *Cerura/Furcula* and *Gluphisia* not only belong together in the same subfamily, the Notodontinae, but that they belong in the same tribe, the Dicranurini (see Table 1). Cremaster morphology provides another synapomorphy in support of my hypothesis.

Base of cremaster fluted. (21) The base of the cremaster in all dioptrine pupae I examined has a characteristic series of longitudinal ridges on its ventral surface. A possibly homologous condition occurs in Nystaleinae, where the cremaster is a different shape than in Dioptrinae but also has longitudinal ridges at its base. Adult and larval data show that these two subfamilies are sister groups (Weller, 1989; Miller, 1991), and I draw attention to this character as another potential synapomorphy.

Cremaster setae. (22) In many families of Lepidoptera there are hook-shaped setae on the cremaster (Fig. 32). These setae can serve either to anchor the pupa to the lining of the cocoon, or in species lacking a cocoon, to attach it to a silk pad on the substrate spun previously by the caterpillar (Common, 1990). There are four pairs of cremaster setae in most Geometridae, and a nomenclature ("D1, D2, L1, SD1")

has been applied to them (e.g., see Bolte, 1990). Presumably, these terms were derived from the primary setal names on the anal plate of larvae (McGuffin, 1987). Although eight is also a typical number of cremaster setae for Notodontidae (see below), I could not homologize those in notodontids with the ones in Geometridae, and so have not applied setal names.

Mosher claimed that presence of hooked setae "is the exception in the Notodontidae, as most of them pupate in the ground" (1916b:58), implying that pupation in the ground obviates the need for setae. I found that hook-shaped cremaster setae occur in six of the nine notodontid subfamilies. Based on my survey, the groups in which they are absent are the Thaumetopoeinae (Fig. 3), Phalerinae (Fig. 26), and Heterocampinae (Fig. 27). Mosher (1918b) used this as diagnostic for Heterocampinae. Among members of the subfamily Notodontinae, setae occur in *Notodonta* (Ferguson, 1963) and other more primitive members of the group, but they are obviously absent in taxa that lack the cremaster altogether (see above).

Where setae do occur, they vary in number from only eight in *Symmerista* and *Notodonta* (Ferguson, 1963) to over 20 in *Platyhasma* (Fig. 5). The outgroup number is about 20 as well (*Doa ampla*, Fig. 2). There is also variation within subfamilies. For example, among the Dioptinae numbers range from eight or ten setae in *Josia* and *Zunacetha* (Figs. 30–32) to about 25 in *Cyanotricha necyria*. *Phryganidia californica* (Dioptinae) is unique in having hook-shaped setae on the dorsum of segments A7–A9, as well as on the cremaster itself (Miller, 1987). The long cremaster of *Clostera* species (Pygaerinae) has a few stout terminal hooks, each bearing tiny setae that Mosher (1918b) noted are easily destroyed and difficult to see.

Body shape:

Body dorso-ventrally compressed. (23) Both Dyar (1891) and Packard (1895) noted that the body of *Cerura* pupae is slightly flattened dorso-ventrally. Packard (1895) also applied that description to the pupae of *Gluphisia* species. He did not, however, use the character as evidence of relationship between the two genera. Although not particularly well-marked in *F. scolopendrina* (Fig. 7B), the trait is readily apparent in other *Furcula* species (Dyar, 1891) as well as in *Cerura*, and it can easily be seen in *Gluphisia septentrionis* (Fig. 8B).

Body wide relative to its length. (24) There is considerable variation in body proportion among the species I studied. I recognized two character states for this trait: in the majority of taxa the body is elongate, while in three taxa—*Thaumetopoea*, *Furcula* and *Gluphisia* (Figs. 3, 7, 8)—the body is wide relative to its length.

CLADISTICS OF PUPAL DATA

Analysis of the data matrix in Table 3, with all nine multistate characters except proboscis length and antenna length (Characters 3 and 5) treated as non-additive, produced a single tree (Fig. 33). There are several important features of that cladogram. First, taxa that I claimed are related based on adult and larval morphology (Miller, 1991) also group together when pupal characters are used. This is a significant result; some of my previous conclusions—such as placement of *Gluphisia* with *Furcula*, and *Crinodes* with *Goacampa*—might be considered controversial.

Second, the subfamily tree based on pupae (Fig. 34) corresponds well with previous hypotheses. For example, two pupal synapomorphies (Characters 16 and 21) unite

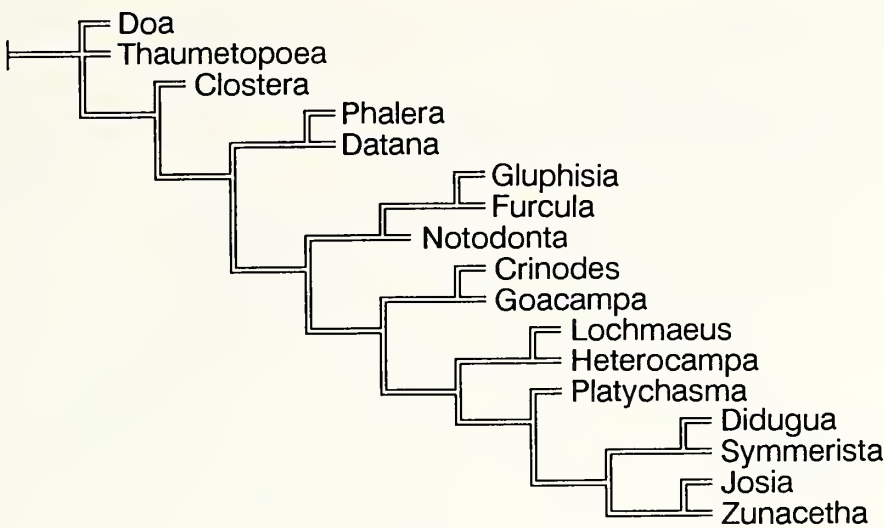


Fig. 33. Cladogram produced by a Hennig86 analysis of 24 pupal characters for 16 species of Notodontidae (see Tables 1, 2) with *Doa ampla* as an outgroup. Length = 52, CI = 71, RI = 80.

the Dioptinae and Nystaleinae, a theory supported by adult and larval data (Weller, 1989; Miller, 1991). Comparison of my adult/larval tree (Fig. 1) with the one from pupae in fact shows only two differences: In the pupal cladogram (Fig. 34), the Phalerinae appear two nodes lower than before, while the subfamily Platychasmatinae has moved higher, appearing as the sister group to the Dioptinae + Nystaleinae.

To further test these comparisons, I combined the 174 characters from my adult/larval matrix (Miller, 1991: appendix IV) for the 17 test species with the 24 pupal characters (Table 3). This produced a single data matrix, containing 198 characters, derived from all three life stages. Analysis of that matrix using Hennig86 and implicit enumeration again gave a single tree (Fig. 35). According to this cladogram, the position of the Phalerinae suggested by pupal morphology (Fig. 34) may be the correct one. On the other hand, the combined analysis supports placement of the Platy-chasmatinae as suggested by adult and larval characters (Fig. 1); rather than being a

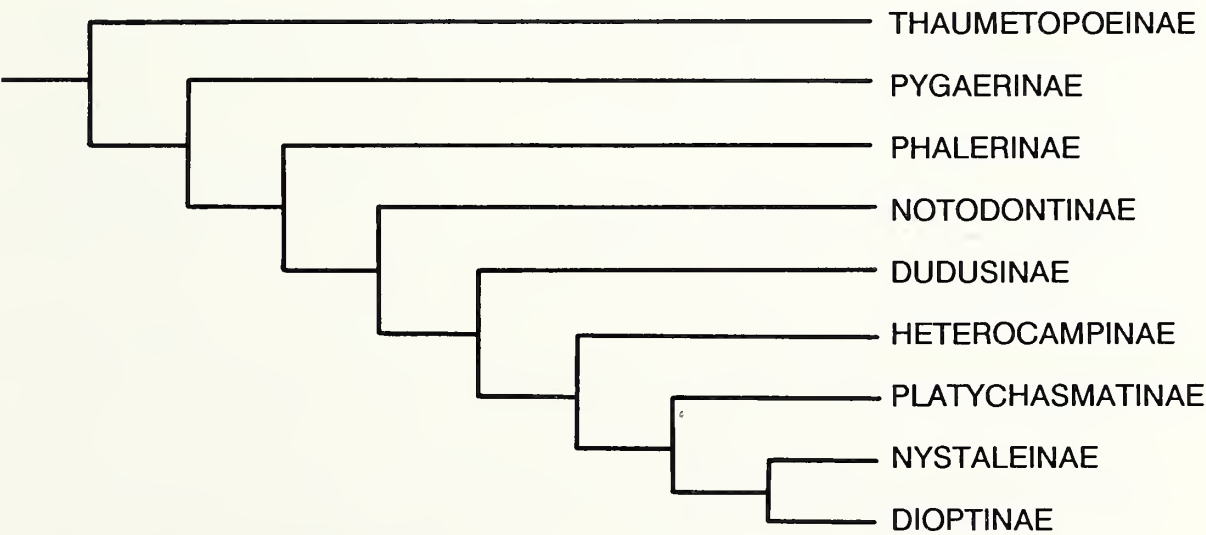


Fig. 34. Relationships among notodontid subfamilies as implied by the cladogram in Figure 33.

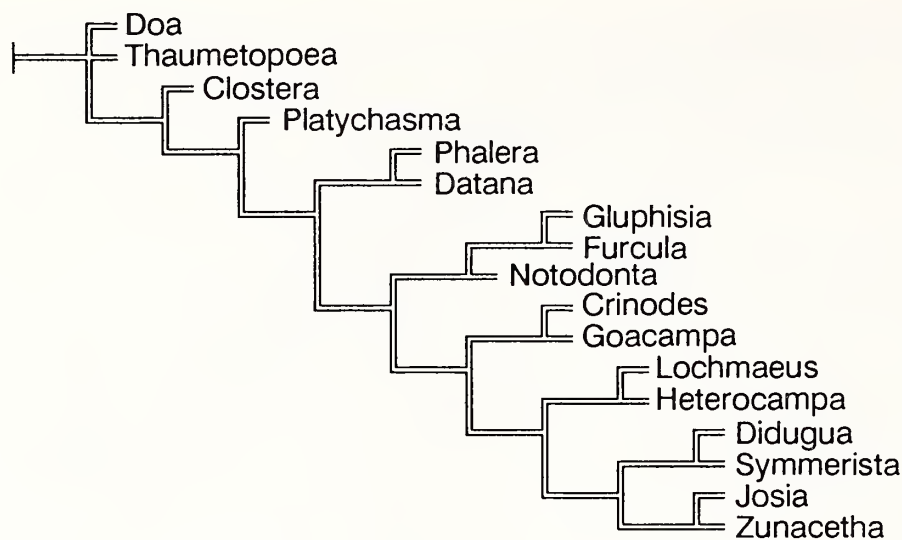


Fig. 35. Cladogram produced by a combined matrix of adult, larval, and pupal characters (total = 198; see text) for 16 species of Notodontidae with *Doa ampla* as an outgroup. Length = 367, CI = 62, RI = 62.

derived group, the Platychasmatinae is the sister-group of all notodontid subfamilies exclusive of the Thaumetopoeinae and Pygaerinae.

Perhaps the most important result of my research on pupal morphology is the discovery of potential synapomorphies for notodontid subfamilies, summarized in Table 4. Clearly, all of my conclusions will be subject to change as pupae from additional notodontid taxa are studied and as more is learned concerning morphology of this life stage.

KEY TO THE PUPAE OF NOTODONTID SUBFAMILIES

Mosher (1918b: 58–60) gives a key to pupae for six North American notodontid genera representing five subfamilies. The key below treats all nine of the currently recognized subfamilies (see Miller, 1991). However, the user should be reminded that it is based on relatively few taxa. In particular, pupae of Neotropical and Old World species may not key out successfully.

- 1. Proximo-lateral angles of proboscis extending to eye-pieces (Figs. 5, 6, 8–12) 4
- Proximo-lateral angles of proboscis not extending to eye-pieces (Figs. 3, 4, 7) 2
- 2(1). Cremaster present; eye-piece not small 3
- Cremaster absent; eye-piece small *Furcula*, *Cerura* (Notodontinae; Fig. 7)
- 3(2). Labial palpi absent; abdominal cuticle covered with fine wrinkles; abdominal spiracles small; body wide; cremaster composed of two horns .. Thaumetopoeinae (Fig. 3)
- Labial palpi present; abdominal cuticle covered with small pits; abdominal spiracles large; body elongate; cremaster a single elongate spine with hooks at tip Pygaerinae (Fig. 4)
- 4(1). Anterior suture of proboscis not strongly curved, arching only slightly forward at midline, proximo-medial angles of proboscis not acute (Figs. 5–8) 5
- Anterior suture of proboscis strongly curved, arching sharply forward at midline, proximo-medial angles of proboscis acute (Figs. 9–12) 7
- 5(4). Antennae extending beyond mesothoracic legs; proboscis as long as wings; forewing venation quadrifid; cremaster with more than 20 hook-shaped setae Platychasmatinae (Fig. 5)

Table 4. Summary of potential subfamily synapomorphies from pupal morphology. Characters are based on study of the species listed in Table 1.

<i>Thaumetopoeinae</i> :	(1) Labial palpus sclerite absent; (2) cremaster setae absent; (3) body wide relative to its length.
<i>Pygaerinae</i> :	(1) Cremaster long and spine-shaped, with stout hooks at tip.
<i>Platychasmatinae</i> :	(1) Forewing venation quadrifid; (2) Antennae extending beyond mesothoracic legs; (2) Dorsum of A10 with numerous, fine longitudinal ridges.
<i>Notodontinae</i> :	(1) Terminal segments of abdomen broadly rounded.
<i>Phalerinae</i> :	(1) Abdomen covered with large, deep pits; (2) Anterio-dorsal margin of A10 with a deep furrow; (3) Cremaster setae absent.
<i>Dudusinae</i> :	(1) Dorsum of thorax with a distinct crest along midline; (2) Caudal margin of mesothorax with a series of shallow depressions separated by longitudinal striations; (3) Anterior margin of each movable segment with a distinct carina.
<i>Heterocampinae</i> :	(1) Caudal margin of mesothorax with a series of small, quadrangular plates separated by deep pits; (2) Anterior margin of each movable abdominal segment ringed with a diffuse band of small pits; (3) Dorsum of A10 with a reticulate area anterior to cremaster; (4) Cremaster fork-shaped, lacking setae.
<i>Nystaleinae</i> :	(1) Labial palpus sclerite present; (2) Thoracic cuticle covered with deep pits; (3) Anterior margin of each movable abdominal segment ringed by a single row of lunate pits.
<i>Dioptinae</i> :	(1) Thorax long, equal to 2/3 total body length; (2) Caudal margin of mesothorax projecting posteriad at body midline; (3) Antennae extremely long, often touching A5; (4) Abdominal spiracles small; (5) Cremaster broad, compressed.

-	Antennae not extending beyond mesothoracic legs; proboscis shorter than wings; forewing venation trifid; cremaster with fewer than 10 setae or with setae absent (Figs. 6–12)	6
6(5).	Terminal abdominal segments (A8–A10) broadly rounded; abdomen covered with small pits; dorsum of A10 unmodified; cremaster often reduced or absent, but when present setae occur	<i>Notodonta</i> , <i>Gluphisia</i> (<i>Notodontinae</i> ; Fig. 8)
-	Terminal abdominal segments tapered; abdomen covered with large, deep pits; dorsum of A10 with a deep furrow; cremaster a series of spines, setae absent	<i>Phalerinae</i> (Figs. 6, 26)
7(4).	Caudal margin of mesothorax strongly sculpted; abdominal spiracles facing laterally; base of cremaster lacking flutes on ventral surface; labial palpi absent (Figs. 9, 10)	8
-	Caudal margin of mesothorax not strongly sculpted; abdominal spiracles facing posteriorly; base of cremaster with longitudinal flutes on ventral surface; labial palpi often present (Figs. 11, 12)	9
8(7).	Caudal margin of mesothorax with a series of shallow depressions separated by raised ridges; thorax with a dorsal crest along midline; anterior margin of each movable abdominal segment (A5–A7) with a carina	<i>Dudusinae</i> (Figs. 9, 14, 23)
-	Caudal margin of mesothorax with a series of small, quadrangular plates separated by deep pits; thorax without a dorsal crest; anterior margin of each movable abdominal segment with a diffuse band of small pits, no carina	<i>Heterocampinae</i> (Figs. 10, 15–18, 21, 27)
9(7).	Surface of thorax deeply pitted; thorax not elongate; mesothorax unmodified; anterior margin of each movable segment with a single row of lunate pits; proboscis only as long as wings; cremaster bifid, not dorso-ventrally compressed	<i>Nystaleinae</i> (Figs. 11, 19, 22, 28)

- Surface of thorax with a few small pits or smooth; thorax elongate, 2/3 the length of abdomen (ventral view); anterior margins of movable segments unmodified; proboscis often longer than wings, touching A5; cremaster dorso-ventrally compressed, not bifid Dioprinae (Figs. 12, 30–32)

DISCUSSION

According to Mosher, “the pupae of [Notodontidae] vary considerably, and there is no one character which will serve to separate them from those of the nearly related families” (1918b:58). None of the diagnostic characters she listed for the Notodontidae (Mosher, 1916b, 1918b) adequately define the group; most are plesiomorphic traits. Both Mosher and Common (1990) emphasized reduction or loss of labial palpi as definitive (see Character 2). Unfortunately, this character is extremely variable among families of Lepidoptera. For example, within the Noctuoidea labial palpi are present in Noctuidae but absent in Arctiidae (Mosher, 1916b). Minet (1991) used reduction of labial palpi in pupae to define a large ditrysian clade that includes the Geometroidea, Hedyloidea, Hesperioidea, and Papilionoidea.

Another pupal trait that Mosher (1916b, 1918b) and Common (1990) stressed in their family diagnoses is presence of punctures on the abdomen. I found, however, that these punctures are absent in *Thaumetopoea pinivora* (representing the subfamily Thaumetopoeinae; see Character 14), so the trait cannot be used to define the Notodontidae. None of the other characters listed by either Mosher or Common can be used as potential family-level synapomorphies.

My own study does little to alleviate this problem; I was unable to find a pupal character unique to the Notodontidae. I can only recommend that future researchers pay attention to morphological detail in the search for a synapomorphy in pupae. If one is to be found, it will not likely involve an obvious feature of the external anatomy. However, lack of a synapomorphy from pupae does not call monophyly of the group into question; there are numerous synapomorphies from adults and larvae (Miller, 1991).

Notwithstanding the problems outlined above, research on pupae makes clear the potential of this life stage for understanding the phylogeny and systematics of the Notodontidae. I have identified pupal traits that elucidate relationships among subfamilies (e.g., Characters 1, 3, 4), as well as traits that help define subfamilies (Table 4). Future research should focus on the pupae of notodontid groups, such as the Hemiceratini, whose positions in the family classification remain enigmatic (see Miller, 1991). Perhaps characters from pupae will provide answers that have not been forthcoming from the study of adults and larvae.

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